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Implications of the Distribution of Albumin Naskapi and Albumin Mexico for New World Prehistory

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ABSTRACT The known distributions of two mutational variants of the albumin gene that are restricted to Mexico and/or North America, Albumin Mexico (AL*Mexico) and Albumin Naskapi (AL*Naskapi), were expanded by the electrophoretic analysis of sera collected from more than 3,500 Native Americans representing several dozen tribal groups. With a few exceptions that could be due to recent, isolated cases of admixture, AL*Naskapi is limited to groups that speak Athapaskan and Algonquian, two widely distributed language families not thought to be related, and to several linguistically unrelated groups geographically proximate to its probable ancestral homeland. Similarly, AL*Mexico is limited to groups that speak Yuman or Uto-Aztecan, two language groups in the American Southwest and Baja California not thought to be closely related to each other, and to several linguistically unrelated groups throughout Mexico. The simultaneous consideration of genetic, historical, linguistic, and archaeological evidence suggests that AL*Naskapi probably originated on the northwestern coast of North America, perhaps in some group ancestral to both Athapaskans and Algonquians, and then spread by migration and admixture to contiguous unrelated, or distantly related, tribal groups. AL*Mexico probably originated in Mexico before 3,000 years BP then spread northward along the Tepiman corridor together with cultural influences to several unrelated groups that participated in the Hohokam culture. Am J Phys Anthropol 111: 557–572, 2000.

Although any population can acquire the language of a genetically unrelated, and, typically, an economically superior group (Nichols, 1992), linguistic similarities among populations are sometimes correlated with genetic similarities (Cavalli-Sforza et al., 1988) and can provide testable hypotheses about common origins of, or historical interaction among, different ethnic groups. Likewise, genetic similarities and differences can provide hypotheses, or support for such hypotheses, regarding genetic relationships among languages. Genetic distances (based on the commonly shared genetic polymorphisms) among some native North American tribes speaking similar languages are smaller than those among groups speaking unrelated languages (Spuhler, 1979; Suarez et al., 1985), suggesting a close relationship between language and genes. However, in other instances, particularly in South America (O'Rourke et al.,

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1992) and less frequently in Mexico and Central America as well (Spuhler, 1979), genetically similar groups speak languages that are not demonstrably related and groups speaking closely related languages exhibit marked genetic differences. Usually, data are lacking for a sufficient number of polymorphisms and/or for sufficiently large samples of populations representing language divisions being compared to assess the correlation between genes and language (Nei et al., 1983).

Some *rare* genetic markers, such as the TF*D CHINESE allele for a variant of the serum protein transferrin and the DI*A allele of the Diego blood group system, are widely distributed, albeit in low frequencies, in many different New World populations (including South America) because they were present in the original colonizers. These markers of Asian, or at least very ancient North American, origin are too ancient to be useful for reconstructing close genetic relationships among New World tribal groups. Other genes with very recent origins, such as Gc*Chippewa (Cleve et al., 1963; Szathmary and Auger, 1983) and the np 16,329 *Rsa*I restriction site loss in mitochondrial DNA (mtDNA) in Athapaskan-speaking groups in the New World (Torroni et al., 1992), exhibit distributions that are too limited to reveal unsuspected genetic relationships. The demonstration of close genetic relationships among Native American tribes not known to share recent common ancestry requires the discovery of marker genes of New World origin that are moderately, but not extremely, ancient. The universal or near-universal sharing of rare genes by all dialects or language subdivisions of two given language families provides strong evidence for either shared ancestry or very ancient admixture which predates the subdivision of at least one (i.e., the younger) of the two language families. Such ancient admixture suggests very special interactions that are themselves of major anthropological interest. The isolated occurrence of a rare mutation of New World origin, in one or a very few subgroups of a larger ethnic group, is more likely to result from admixture than common ancestry. While reliably selecting between the two possible explanations for sharing a rare allele at a single locus requires a much larger and more representative sample of related tribal groups than is typically available, the distribution of rare alleles acquired by recent admixture is not likely to exhibit genetic equilibrium with respect to alleles at other independent loci.

Albumin Naskapi, AL*Naskapi (Melartin and Blumberg, 1966), has been found, albeit in low frequency, in all Athapaskan-speaking (but not in Tlingit, whose language is related to Athapaskan: Leer, 1990) and Algonquian-speaking groups, with the exception of the Micmac, for which a sufficiently large sample of sera has been screened, including the Blackfoot (see Schell and Blumberg, 1988, for a review of its previously known distribution), whose language is the most divergent of all Algonquian languages (Goddard, 1994). The allele has seldom been reported in samples drawn from any non-Athapaskan/non-Algonquian group. The presence of AL*Naskapi in very low frequency in one, or a very few, Siouan (e.g., Assiniboin), Yuman (Mohave, Maricopa), Uto-Aztecan (e.g., Hopi), and Eskimo-Aleut groups in close geographic proximity to, or which experienced close ethnohistorical relationships with, an Athapaskan or Algonquian group has been reported, but recent admixture, rather than recent common ancestry, is probably responsible. AL*Naskapi (an A $\rightarrow$ G transition at the end of the ninth exon of the albumin gene, leading to the substitution of lysine for glutamic acid in the albumin molecule) is identical to two other rare mutations, found in Southeastern Turkey (Franklin et al., 1980) and North India (Kaur et al., 1982). Although mtDNA haplogroup X, another rare trait, has a similar distribution and might suggest an Old World origin for both (Comas et al., 1996), all three albumin mutations might have independent origins (Takahashi et al., 1987), as has been demonstrated for other structurally identical albumin mutations (Huss et al., 1988; Brennan et al., 1990).

The apparent regularity with which Athapaskan and Algonquian groups share AL*Naskapi suggests either 1) a close genetic relationship between these two

groups, which is not consistent with either linguistic evidence (Goddard, 1996; Campbell and Mithun, 1979; Campbell, 1997) or with phenograms based on many shared polymorphisms (Szathmáry, 1993; her Fig. 4), 2) gene flow from a subdivision of one of these two language groups into the ancestral (founding) population of the other language group before its subdivision, which is difficult to reconcile with the early historic geographic distributions of the tribes of these two language stocks, or 3) that AL*Naskapi is a very ancient mutation in Native Americans that survived only in Athapaskan and Algonquians. The first and the last of these three alternatives imply that both Athapaskans and Algonquians descend from the same founder population. It is also conceivable that this mutation occurred independently in Athapaskans and Algonquians or was acquired by each from separate Asian origins, but, as with the third alternative cited above, the contiguity of their respective geographic distributions and the low worldwide frequency of the mutation make this coincidence seem too incredible to be likely. It is difficult to select among alternative hypotheses regarding the distribution of AL*Naskapi because key information about that distribution is lacking. The albumin polymorphism has not been screened for Algonquian-speaking groups south of the 49° North latitudinal parallel or for other groups whose languages, such as Salish and Wakashan on the one hand and Haida on the other, have been hypothesized (albeit not substantiated; see Campbell, 1997) to be related to Algonquian and to Athapaskan, respectively (Sapir, 1929; Greenberg, 1987). This is important because AL*Naskapi is more likely to have originated in that language group whose more remote members also exhibit that mutation.

The geographic distribution of AL*Mexico (Melartin et al., 1967), another albumin mutation of apparent New World origin, is more complex and even less well-known than that of AL*Naskapi. AL*Mexico has been reported, again in low frequency, in all major language groups of Mexico. In North America, AL*Mexico is limited to the southwestern U.S., where it has been reported in some (e.g., Pima, Papago, and Ute) but not all (e.g., Hopi) Uto-Aztecan-speaking groups that have been studied, in Zuni which is either a language isolate or a language whose affiliation is uncertain, in both divisions of southern Athapaskan (Apachean), Navaho and Apache, and in three River/Delta Yuman-speaking groups (Cocopah, Maricopa, and Mohave). Two of the three River/Delta Yuman-speaking groups with AL*Mexico (unlike any other non-Athapaskan group that also carries AL*Mexico) also carry AL*Naskapi, albeit in very low frequency (Schell and Blumberg, 1988), suggesting admixture with Athapaskans (probably western Apache who lived immediately east of these Yuman-speakers); it is therefore probable that Athapaskans themselves acquired AL*Mexico by admixture with Yumans rather than with Pimans, who themselves lack AL*Naskapi (Schell and Blumberg, 1988). AL*Mexico has been found to be absent in all Native American tribes of Alaska and Canada (i.e., Eskimo/Aleut, Athapaskans, and Canadian Algonquians), the United States east of the Rocky Mountains (e.g., U.S. Algonquian, Iroquoian, Assiniboin, Omaha, Dakota Sioux, and Seminole), and South America that have been studied.

The occurrence of AL*Mexico in Aztecan (or Nahuatlan), Sonoran, and Shoshonean languages, the three major geographic branches of the Uto-Aztecan language family (Miller, 1984), is consistent with the expectation that all speakers of Uto-Aztecan are closely genetically related. The occurrence of AL*Mexico in southern Athapaskans (Apache and Navaho), Yumans, Huasteco, Zuni, and Tarascan (a Chibchan language), whose languages are not known to be related, could represent either admixture or very remote common ancestry with Uto-Aztecans. While AL*Mexico (or AL*Naskapi) could have an ancient origin and might have become extinct in many Native American groups in which it once existed, it is improbable that the few groups that retain the trait would be mutually geographically contiguous and/or linguistically related. Since too few tribal groups of North America have been screened for albumin polymorphisms to assess alternative explanations for their

distribution, we studied several widely geographically dispersed groups in which the albumin phenotypes have not been reported as well as several groups nearby or closely related to those known to carry AL*Mexico or AL*Naskapi. These include: 1) Upland Yuman groups (e.g., Yavapai, Hualapai, Havasupai) and those of Baja California (e.g., Pai Pai, Kumiai, Cucapa), who are less likely than the River Yumans of the U.S. (who exhibit relatively high frequencies of AL*Mexico but are known to have interacted closely with Pimans in historic times) to have acquired AL*Mexico by recent admixture from Uto-Aztecan neighbors such as the Pima or from any other groups (e.g., Wormington, 1970), 2) the Kiliwa and Cochimi, two tribal groups of Baja California that are more closely related to Yumans than to any other groups, and the Washo, who are believed to be more remotely related to Yumans (Kaufman, 1988), 3) Great Basin groups (e.g., Paiute, Shoshone) affiliated with the northern (or Shoshonean) branch of the Uto-Aztecan language stock, which includes Ute from which a single copy of AL*Mexico has been reported (Johnston et al., 1969), 4) the Jemez Pueblo whose language (Tanoan) has been hypothesized to be related, albeit remotely, to Uto-Aztecan (Whorf and Trager, 1937; Davis, 1989), 5) most groups of the Plains (e.g., Siouan-speaking groups) and lands east of the Rocky Mountains (e.g., the Iroquoian-speaking Cherokee and the Muskogean-speaking groups, such as Chickasaw, Choctaw, and Creek, of the southeastern U.S.) who have ties to groups known to carry AL*Naskapi or who live contiguous to such groups, 6) language groups of the Northwest such as Salishan and Wakashan, whose relationships both to each other (e.g., see Swadesh, 1953a,b) and to Algonquian (e.g., see discussion of the "Almosan" proposal in Campbell, 1997) are controversial, and 7) Algonquian-speaking tribes of the U.S. (e.g., Cheyenne/Arapaho).

In this paper we report the presence or absence of AL*Mexico and AL*Naskapi in several groups not previously studied and provide a preliminary comparison of mtDNA control region (CR) sequences and haplogroup frequency distributions among groups sharing at least one of these two mutations. Groups that share a rare variant due to common ancestry are more likely to exhibit similar mtDNA sequences and haplogroup frequency distributions than are groups sharing a rare variant that is very widely distributed or groups all but one of which acquired the variant by admixture. Moreover, in such groups the distributions of AL*Naskapi (or AL*Mexico) and the common allele, AL*A, should exhibit equilibrium with respect to the mtDNA haplogroups.

METHODS

The serum samples included in the present study and their sources are described in Table 1, and most have been cited elsewhere (Lorenz and Smith, 1994, 1996, 1997). Tribes whose language groups are not closely related to that of any other group that has previously been screened for albumin polymorphism are indicated by asterisks. None of the more than three dozen specific tribes, bands, or communities listed in Table 1, except the San Carlos Apache, have previously been screened for albumin polymorphism. This group is included because it was anticipated that it would be useful for assessing equilibrium between the albumin and mtDNA loci. Some of the population samples reported in Table 1 represent more than one tribal group speaking closely related dialects or languages. Samples from these groups were combined in Table 1 because 1) extensive admixture among these groups is known to have occurred (e.g., the Cheyenne/Arapaho and the three Muskogean-speaking tribes), 2) very few samples were available and no variation in the presence or absence of AL*Mexico or AL*Naskapi was found (e.g., "other Algonquian" and "Southern Sioux"), or 3) subjects failed to acknowledge or report their affiliation with a single tribal subdivision (e.g., Sisseton/Wahpeton Sioux).

After arrival in dry ice, all serum samples were frozen at −20°C until they were thawed for electrophoretic analysis or DNA extraction. When the sera were thawed, 10 μl of a 1:100 dilution (in dH_2O with 30% sucrose) were added to wells of a 10% Tris-sulfate, pH 9.0, polyacrylamide gel and the

TABLE 1. Populations sampled and their linguistic affiliations

Linguistic affiliation	Tribe, population, or settlement	*N*	Number heterozygous Al *Naskapi	Number heterozygous Al *Mexico	Source
Eskimo					
Inuit	Inuit	104	0	0	Dr. Henry Gershowitz, Department of Human Genetics, University of Michigan, Ann Arbor, MI
Greenland	Augpilogtok Island	80	0	0	Dr. Arthur Steinberg, Department of Biology, Case Western Reserve University, Cleveland, OH
Algonquian					
Cheyenne/Arapaho[1]	Arapaho and Southern Cheyenne	40	2	1	Dr. Vincent Henderson, Public Health Service Indian Hospital, Concho, OK
Chippewa					
	Salteaux (Turtle Mt.)[1]	189	4	0	Dr. Lyle Best, Public Health Service Indian Hospital, Belcourt, ND
	Lac Courte Oreilles[1]	95	2	0	Ms. Michelle Boudin, Lac Courte Oreilles Community Health Center, Hayward, WI
	Mille Lacs[1]	28	1	0	Ms. Gert Lambert, Ne-ia Shing Indian Health Service Clinic, Onamia, MN
Other		30	0	0	Various sources
Salish (Coast)[1]	Bella Coola	111	11	0	Dr. L.L. Field, Department of Pediatrics, University of Calgary, Calgary, Alberta, Canada
Wakashan[1]	Nootka	257	1	0	Dr. R.H. Ward, Department of Human Genetics, University of Utah, Salt Lake City, UT
Iroquoian	Cherokee (Oklahoma)	215	0	0	Dr. D.O. Kasprisin, American Red Cross, Tulsa, OK, and Ms. Beverly Stone, Cherokee Nation Indian Health Clinic, Stilwell, OK
Siouan					
	Sisseton/Wahpeton[1]	91	3	0	Mr. Jerome DeWolfe, Fort Totten Health Center, Fort Totten, ND
	"Southern Sioux" (Iowa, Ponca, Quapaw, Winnebago)	14	0	0	Various sources
Athapaskan					
Dogrib	Rea Band	69	2	0	Dr. Robert E. Ferrell, Department of Biostatistics, University of Pittsburgh, Pittsburgh, PA
Apache	Western (San Carlos)	520	18	39	Dr. Peter Bennett, National Institute of Arthritis and Metabolic Diseases, Phoenix, AZ
Navaho					
	Bloomfield[1]	100	8	0	
	Keams Canyon[1]	192	11	2	Dr. Henry Gershowitz
Haida	Queen Charlotte Island	69	0	0	Dr. L.L. Field
Muskogean	Chickasaw,[1] Creek,[1] Choctaw[1]	119	0	0	Dr. D. Kasprisin and Dr. Douglas Forman, Chickasaw Nation Health Clinic, Ardmore, OK
Hokan					
Washo[1]	Washo	133	0	0	Dr. Peter Bennett
Cochimi[1]	La Heurta and San Antonio Necua, Baja	30	0	0	Dr. Hector Velasquez, University of Baja California Medical School, Mexicali, Mexico
Kiliwa[1]	Arroya de Leon, Baja	11	0	2	Dr. Hector Velasquez
Yuman					
Delta	Kumiai, Cucapa (Baja)[1]	40	0	0	Dr. Hector Velasquez
River	Quechan[1]	143	0	9	Dr. Peter Bennett
Pai[1]					
	Pai Pai (Santa Catarina, Baja)	20	0	1	Dr. Hector Velasquez
	Havasupai	90	0	0	Dr. Peter Bennett
	Hualapai	214	0	4	Dr. Peter Bennett
	Yavapai	115	0	5	Dr. Peter Bennett
Tanoan[1]	Jemez Pueblo	77	0	0	Dr. Gerald Ross, Jemez Indian Health Center, Jemez Pueblo, NM
Uto-Aztecan					
Shoshone[1]	Snake	30	0	1	Dr. Peter Bennett
Paiute (Northern)[1]	Walker River	165	0	0	Dr. Peter Bennett
Pima	Pima	151	0	8	Dr. Arthur Steinberg
Nahuatle	Nahua	68	0	0	Dr. Ruben Lisker, National Institute of Nutrition, Mexico City, Mexico
Zuni	Zuni	202	0	0	Dr. Henry Gershowitz

[1] Language group no representative sample of which has previously been studied for albumin polymorphism.

proteins were separated at 300 V and at 4°C for about 5 hr using a Tris-borate running buffer (Smith, 1980). The gel buffer contained 18.15 g Tris, 31 ml 1 N H_2 SO_4, and 0.24 ml TEMED per 100 ml dH_2O. The running buffer, also pH 9.0, contained 7.86 g Tris and 1.09 g boric acid per liter of dH_2O. The gels were stained for 3–5 hr with 100 ml of a solution containing 400 mg Coomassie blue G-250, 30.5 ml 70% perchloric acid, and 970 ml dH_2O (Holbrook and Leaver, 1976) and destained overnight, with rotation, in 5% glacial acetic acid.

Two-hundred eighty-four base pairs (bp) of the mtDNA CR sequence were compared between pairs of all major tribes exhibiting AL*Naskapi or AL*Mexico to evaluate the likelihood that common ancestry is responsible for the distribution of these mutations. Thirty of these sequences were characterized, using methods previously described in Lorenz and Smith (1997), after amplification from sera screened for albumin polymorphism, and a greater number were taken from the literature cited in that paper. The average numbers of differences between all possible pairs of sequences from different tribal groups that exhibit one of the albumin mutations were computed. Separate estimates were also made based only on the smaller numbers of paired samples that are members of the same mtDNA haplogroup. The frequency distributions of mtDNA haplogroups of these same pairs of ethnic groups, most of which were published previously (Lorenz and Smith, 1996), were also compared using the contingency chi-square test for homogeneity and also represent a sample of those screened for albumin polymorphism.

DNA was extracted from samples exhibiting AL*Naskapi or AL*Mexico and assigned a haplogroup affiliation, using the same methods described for samples homozygous for AL*A that were previously published (Lorenz and Smith, 1996). The mtDNA haplogroup distributions of both Algonquians and Athapaskans (Apacheans; Apache and Navaho) with and without AL*Naskapi and those of Yumans, Pimans, and Apacheans with and without AL*Mexico were compared to determine whether or not the two loci were in equilibrium. If relatively recent admixture is responsible for the presence of AL*Naskapi in either Athapaskans or Algonquians, the genotypes at the albumin locus should not have reached equilibrium with the mtDNA haplogroups in that group. In contrast, if the presence of AL*Mexico in the Apache results from their acquisition of Yuman (or Piman) wives as we have hypothesized (Lorenz and Smith, 1996), it should more frequently appear in Apache samples that also exhibit mtDNA haplogroups that are more common in Yumans (or Pimans, i.e., haplogroup B and, less frequently, haplogroup C) than in samples that are members of haplogroup A which is rare in non-Apacheans in the American Southwest (though it is common in Mesoamerica). Equilibrium between the albumin and mtDNA loci was assessed using a contingency chi-square with the highest number of degrees of freedom that allow a valid statistical test (Siegel and Castellan, 1988). For this test, the number(s) of samples heterozygous for AL*Naskapi or AL*Mexico that exhibited the most commonly occurring (or the two most commonly occurring) mtDNA haplogroup(s) was (were) compared with that for heterozygous samples assigned to all other (less common) haplogroups combined.

RESULTS

The numbers of samples screened that were heterozygous for AL*Naskapi and for AL*Mexico are given in Table 1 by language affiliation. No samples were found that were either homozygous for either mutation or heterozygous AL*Naskapi/AL*Mexico. In accordance with previous studies, both AL*Naskapi and AL*Mexico were absent among Eskimo and Haida and present among southern Athapaskans. Earlier reports of AL*Mexico in Zuni (Brown and Johnson, 1970) and Nahua (Lisker et al., 1971) could not be confirmed by this study, perhaps due to the restricted sample sizes or to sampling error in the present study. The absence of both mutations among the Cherokee is consistent with their reported absence among the Mohawk, also an Iroquoian-speaking group, but AL*Naskapi was present in three Siouan individuals whose language has been hypothesized, but

*TABLE 2. Average number of base substitutions (of 284) in the mtDNA control region differentiating group-specific lineages[1] between, and distribution of mtDNA haplogroups[2] in, pairs of six ethnic groups[3] with AL*Naskapi or AL*Mexico[4]*

	Algonquian (4) [61, 13, 46, 7, 45]	Athapaskan (10) [42, 0, 0, 0, 0]	Bella Coola (19) [18, 2, 5, 9, 2]	Nootka (27) [6, 1, 2, 4, 2]	Uto-Aztecan (10) [North, 0, 48, 16, 49, 7] [Central, 2, 27, 14, 0, 0] [South, 17, 11, 2, 0, 2]	Yuman (8) [3, 50, 27, 0, 1]
Algonquian		6.75 (40)	7.20 (76)	6.35 (108)	7.20 (40)	7.38 (32)
Athapaskan	5.00 (19)		6.25 (190)	5.30 (270)	8.22 (90)	9.15 (80)
Bella Coola	5.50 (34)	5.53 (137)		6.11 (513)	8.15 (190)	9.26 (152)
Nootka	4.13 (54)	3.70 (194)	4.38 (327)		6.73 (270)	8.19 (216)
Uto-Aztecan	4.70 (13)	4.69 (32)	4.39 (59)	3.10 (87)		7.14 (80)
Yuman	4.25 (8)	4.00 (2)	3.25 (16)	4.00 (12)	4.18 (22)	

[1] Numbers above diagonal are irrespective of haplogroup affiliation; those below diagonal refer only to pairs of sequences that are members of the same mtDNA haplogroup. Numbers in parentheses are total numbers of paired sequences used to calculate the average number of base substitutions.
[2] Number of individuals of each ethnic group sampled that are members of haplogroups A, B, C, D, and "other," respectively, are given in brackets below the appropriate ethnic group. Those individuals included in the D-loop sequences that are compared represent a subset of those whose haplogroup distributions are reported here.
[3] Haplogroup distributions of Uto-Aztecans are subdivided into North (Northern Paiute and Shoshone), Central (Pima, Papago, Hopi, Comanche), and South (Nahua and Cora). The Athapaskan, Bella Coola, and Nootka samples are represented by a single tribe, the Algonquian sample includes seven different tribes, and the Yuman sample includes 10 different tribes.
[4] These data are taken from Lorenz and Smith (1996, 1997).

not proven (e.g., see discussion of the Macrosiouan hypothesis in Campbell, 1997) to be related to Iroquian (Allen, 1931; Chafe, 1973). AL*Naskapi was present in all four Algonquian groups studied (but not in a miscellaneous group of "other" (predominantly Eastern) Algonquians) and in two groups (Bella Coola and Nootka) whose languages were previously hypothesized to be remotely related both to each other (Swadesh, 1953a,b) and to Algonquian (Sapir, 1929). AL*Mexico occurred in 4 of the 7 Yuman-speaking groups studied and in Kiliwa, a closely related group, but not in Cochima, another group whose language is closely related to Yuman, or in Washoe, which is hypothesized to be more remotely related (linguistically) to Yuman (Kaufman, 1988). While AL*Mexico, as expected, was common among the Pima of the Southwest U.S., it was absent among both the Nahua of Mexico and the Northern Paiute of the western Great Basin, both of whose (Uto-Aztecan) languages are closely related to Piman.

As shown in Table 2, the mtDNA haplogroup distribution of Yumans is very similar to that of the Pimans (i.e., the Central, or Sonoran, division of Uto-Aztecan; $\chi^2 = 0.09$, with 3 df) but significantly different from those of both Shoshoneans ($\chi^2 = 46.5$) and Nahua ($\chi^2 = 41.8$) who, respectively, represent the northernmost and southernmost divisions of the Uto-Aztecan language family. The mtDNA haplogroup distribution of Athapaskans, in which haplogroup A predominates, was very statistically significantly different ($P \ll 0.0001$) from those of all other ethnic groups, but those of Algonquians, Bella Coola, and Nootka were all very similar (χ^2, with 1 df, $P < 0.35$ for all three comparisons). Mean pairwise sequence differences between tribal groups exhibiting AL*Naskapi or AL*Mexico are also given in Table 2. The average number of sequence differences between the major groups carrying AL*Mexico (Uto-Aztecans and Yumans) and AL*Naskapi (Algonquians and Athapaskan) were 7.14 and 6.35, respectively. The average number of sequence differences between groups carrying different albumin mutations was higher, at 8.04, as would be expected of less closely related groups. However, the average numbers of paired sequence differences between groups are strongly influenced by among-group differences in haplogroup frequency distributions (Lorenz and Smith, 1997), which can themselves be influenced by genetic drift. Thus, when comparisons between samples belonging to the same haplogroups only are considered, both Uto-Aztecans (as a group) and Yumans were more closely related to at least one of the groups exhibiting AL*Naskapi than they were to each other. Similarly, the mtDNA CR sequences of Algonquians and Athapaskans were each more similar to those of both

TABLE 3. Distribution of genotypes at the albumin locus by mitochondrial DNA haplogroup

Language group	Albumin genotype	mtDNA haplogroup				
		A	B	C	D	X
Apachean	AL*A/AL*A	48	29	6	2	2
	AL*A/AL*Naskapi	16	9	4	0	?
	AL*A/AL*Mexico	15	2	18	0	0
Algonquian	AL*A/AL*A	98	18	62	9	48
	AL*A/AL*Naskapi	3	0	3	1	3
Bella Coola	AL*A/AL*A	18	2	5	9	0
	AL*A/AL*Naskapi	6	0	0	0	0
Yuman	AL*A/AL*A	3	50	27	0	0
	AL*A/AL*Mexico	3	5	0	0	0
Piman	AL*A/AL*A	2	21	14	0	0
	AL*A/AL*Mexico	0	4	2	0	0

Uto-Aztecans and Yumans than they were to those of each other.

The distribution of mtDNA haplogroups among the members of the indicated tribes that are heterozygous for AL*Naskapi and AL*Mexico and homozygous for AL*A are given in Table 3. Of 29 Apachean (Southern Athapaskan) samples that carried AL*Naskapi, 16 were A and 13 were other haplogroups (9 and 4 individuals, respectively, were haplogroup B and C), while 16.64 and 12.36, respectively, were expected based on the distribution of haplogroups among Southern Athapaskans lacking AL*Naskapi or AL*Mexico. Likewise, of 10 Algonquians with AL*Naskapi, 3 were assigned to haplogroup A, while 7 were assigned to other haplogroups (3 each to haplogroups C and X and 1 to haplogroup D), while 4.42 and 5.62 were expected under equilibrium conditions. AL*Naskapi was in equilibrium with the mtDNA haplogroup distribution in both Algonquians ($\chi^2 = 0.33$) and Athapaskans ($\chi^2 = 0.00$). The very few Piman samples heterozygous for AL*Mexico whose mtDNA haplogroups could be determined could not provide a valid statistical test but exhibited no evidence of disequilibrium between these two loci. In contrast, the distribution of albumin genotypes among Apacheans with haplogroup A, haplogroup B, and all other haplogroups was statistically significantly heterogeneous between albumin phenotypes (χ^2 with 2 degrees of freedom = 25.7, $P \ll 0.0001$), with haplogroups other than A or B exhibiting an excess of heterozygosity for AL*Mexico. In addition, AL*Naskapi appeared not to be in equilibrium with the mtDNA haplogroups in the Bella Coola, and AL*Mexico appeared not to exhibit equilibrium with respect to the distribution of mtDNA haplogroups in the Yumans. Both Yumans with AL*Mexico and Bella Coola with AL*Naskapi appeared to exhibit an excess of haplogroup A. However, sample sizes of heterozygotes for the albumin locus whose mtDNA haplogroups could be determined for these two groups were inadequate to provide valid statistical tests.

DISCUSSION

Since sample sizes for some groups were quite small, sampling error might be responsible for the absence of AL*Naskapi or AL*Mexico in some groups. AL*Mexico might also have been lost in these groups through genetic drift, since the population sizes of some of these groups have been quite small for several centuries. The prevalence of AL*Naskapi in Athapaskan-speaking and Algonquian-speaking tribes in this study is consistent with previously published reports (see Schell and Blumberg, 1988). In addition, two samples drawn from fullblood southern Cheyenne Indians were found to be heterozygous for AL*Naskapi and represent the first report of AL*Naskapi in Algonquians of the U.S. other than the Blackfoot and Chippewa.

Implications of the distribution of AL*Naskapi

If Athapaskans and Algonquians are descendants of two separate migrations to the New World or descend from founders who are not closely related, as suggested by some linguistic (e.g., see Campbell, 1997) and ge-

netic (Torroni et al., 1992) evidence, one of these two groups must have acquired AL*Naskapi through admixture with the other. The one of these two groups (Athapaskan or Algonquian) that dispersed into smaller groups earlier than the other is more likely to have been the source, rather than the recipient, of AL*Naskapi. Glottochronological analysis (Swadesh, 1971) cannot ensure precise estimates of the time of separation of two related languages (Campbell, 1997), but can provide relative ages of different protolanguages. The languages spoken by the several Algonquian groups in which AL*Naskapi has been found derive from a protolanguage estimated to be about twice as old as the proto-Athapaskan language (e.g., compare the estimate of Krauss (1973) of about 2,000 years BP for Athapaskan with that of Denny (1991) of about 4,000 years BP for Algonquian), and proto-Athapaskan was still spoken after the tribal groups speaking Algonquian languages were already geographically dispersed. This suggests that an Algonquian origin of AL*Naskapi is more plausible than an Athapaskan one. The dispersal of Athapaskan at a time after the hypothesized date when Algonquians abandoned the Columbia Plateau and the absence of AL*Naskapi in groups that speak languages related to Athapaskan, such as Tlingit, or purportedly related, as Haida, also support this hypothesis. However, the absence, or near absence, of mtDNA haplogroups C and X, which are common in all Algonquians, in Athapaskans (Lorenz and Smith, 1997; Smith et al., 1999) and the preponderance of females among adult slaves captured by tribes in the region (e.g., see Drucker, 1965) are not compatible with this hypothesis and suggest that common ancestry between the two groups is responsible for their sharing of this mutation. This explanation is consistent with the general correlation between geographic proximity and genetic relationships among Native American tribes and with gene frequency maps based on protein-coding loci (Suarez et al., 1985) and with the simultaneous sharing of the relatively rare mtDNA haplotype X (Brown et al., 1998; Smith et al., 1999) and the Y-chromosome haplotype 1F (Karafet et al., 1999) by very few Native American groups other than Athapaskans and Algonquians. This evidence that Algonquians and Athapaskans share a common founding ancestral origin adds further credence to the single-migration hypothesis for peopling of the New World that has drawn recent support from genetic studies (Merriwether et al., 1995; Lorenz and Smith, 1997; Stone and Stoneking, 1998). The relatively high average number of base substitutions differentiating members of these two different language families might result from their different histories of admixture with different tribes and/or the rapid population growth of both groups after Algonquians migrated eastward from their homeland on the Columbia Plateau, about 4,000 years BP.

The data presented here also represent the first report of AL*Naskapi in non-Athapaskan tribes of the Northwest coast. Serum samples drawn from the Bella Coola and Nootka, who speak Salish and Wakashan languages, respectively, yielded 11 individuals and 1 individual, respectively, heterozygous for AL*Naskapi. This outcome and the very close similarity among the mtDNA haplogroup distributions of Algonquian, Bella Coola, and Nootka, shown in Table 2, are consistent with the controversial argument by Sapir (1929) that Algonquian, Salish, and Wakashan languages comprise a language group (Almosan) whose speakers are related (see Kinkade (1990) for a discussion of the history of classification of Northwest coast languages). The Nootka and Bella Coola, who comprise the hypothetical "Mosan" language group, once defended but then abandoned by Swadesh (1953a,b), share at least two mtDNA CR sequence lineages in common with each other (albeit one of these is also common in Athapaskans, but not in Algonquians), and the sequence data in Table 2 do not suggest that this similarity is necessarily the result of common ancestry rather than admixture. The sequences of both Bella Coola and Nootka are also more closely related to those of at least one of the two groups studied that carry AL*Mexico than to those of each other or than either is to those of any other group studied here, including Algonquian, that carries

AL*Naskapi. Although a larger sample of sequences from these groups should be studied to assess the genetic relationships implied by the "Mosan" hypothesis (Swadesh, 1953a,b), neither the common presence of AL*Naskapi nor the mtDNA evidence is consistent with it. In fact, Denny (1991) recently concluded that the sound correspondences he once cited as evidence for a genetic relationship between the Algonquian and Salishan languages are in fact due to borrowing rather than common ancestry. The results of our study of genetic equilibrium between the albumin and mtDNA loci are also consistent with this interpretation. Of 7 Bella Coola samples with AL*Naskapi from which DNA could be extracted, 6 belonged to haplogroup A (one belonged to a European haplogroup, the result of admixture), which is nearly fixed in Northern Athapaskan groups, while only half of the Bella Coola samples homozygous for AL*A belong to haplogroup A (Lorenz and Smith, 1996). Thus, it seems likely that the albumin locus is not in equilibrium with the mtDNA genome in Bella Coola because the presence of AL*Naskapi is due to recent admixture with Northern Athapaskans, in whom almost all members with AL*Naskapi are also members of haplogroup A.

The discovery of three fullblood Sisseton/Wahpeton Sioux samples heterozygous for AL*Naskapi is consistent with an earlier study reporting the presence of AL*Naskapi in one member of the Assiniboin tribe (an offshoot of the Yantonai, or central Sioux) and in two Sioux whose tribal affiliation is unknown (Schell and Blumberg, 1988). The presence of AL*Naskapi in three different geographically dispersed Siouan tribes suggests that its presence might be due to either common ancestry or very early and extensive admixture of proto-Siouan groups with Algonquians or with other groups that carry AL*Naskapi. The sharing of haplogroup X, the rarest of all mtDNA haplogroups in North American, among Algonquians, Athapaskans, and Siouans (Brown et al., 1998; Smith et al., 1999; Bianchi and Bailliet, 1997), is also consistent with either of these two hypotheses. Common ancestry between Siouan and Algonquian would be consistent with the hypothesis of Greenberg (1987) of a genetic relationship (albeit very remote) between the Keresiouan and Algonquian languages, a view not previously proposed, even by Sapir (1929). However, AL*Naskapi (as well as haplogroup X) is absent among the Iroquoian-speaking Mohawk (Schell et al., 1978) and Cherokee (in this study), whose languages have been hypothesized to be related to Siouan languages (Allen, 1931; Chafe, 1973); Siouan languages probably originated far southeast of the homelands of the Athapaskans and Algonquians (Nichols, 1998), making recent common ancestry less likely. Very recent admixture could be responsible for the occurrence of AL*Naskapi (as well as haplogroup X) in some Siouan groups, because the Assiniboin have historically lived in close contact with the Cree (Algonquians) to their north who also carry AL*Naskapi, and the eastern Sioux were in close contact with Algonquian-speaking tribes to their east, that are closely related to tribes known to carry AL*Naskapi. Moreover, we have recently reported the HVS-I sequence of a Sisseton-Wahpeton Sioux, assigned to haplogroup X, who also exhibited Albumin*Naskapi. Since the simultaneous occurrence of these two traits is rare in Sioux but common in Algonquians, the presence of both traits in Plains Sioux is more likely to result from recent admixture than from common ancestry with Algonquians. Much earlier admixture might have resulted from contacts with Algonquians during their eastward migration from the Columbia plateau to the southern border of Lake Michigan (Denny, 1991; Goddard, 1994; Nichols, 1998), after which time Algonquians, and/or their language, dispersed further eastward, and then northward into the Subarctic (Siebert, 1967). Since the core Siouan languages diverged about 3,000 years BP (Rankin, 1993), the Plains Sioux might have been a single homogeneous group when the hypothetical Algonquian migration resulted in contact with proto-Siouan groups migrating northwestward onto the Plains from their homeland (in the southeastern U.S.? see Nichols, 1998). This explanation is consistent with a northwest coast origin of AL*Naskapi.

Other features of the distribution of AL*Naskapi in North America more clearly reflect the importance of admixture among Native American tribes. Both ethnographic (Brugge, 1983) and early blood group (Brown et al., 1958) studies suggest that Western Apache admixture in the American Southwest was predominantly with Yuman and Piman tribes to the West, while Navaho admixture was predominantly with Pueblo groups to the east that lacked AL*Mexico. Thus, the isolated occurrence of AL*Naskapi in both Yuman (e.g., Mohave and Maricopa) and Uto-Aztecan (e.g., Hopi) groups (Johnston et al., 1969; Franklin et al., 1980) is almost certainly due to recent admixture with western Apache and Navaho groups, respectively. The western Apache and the Navaho, in turn, probably acquired AL*Mexico, as well as mtDNA haplogroup B (Lorenz and Smith, 1994, 1996), by admixture with Yuman-speaking and Pueblo groups, respectively (most Pueblo groups, including the Hopi, lack AL*Mexico; the Pima, the only other abundant source of AL*Mexico other than Yumans, lack AL*Naskapi), when they reached the southwest within the last millennium (Brugge, 1983).

Implications of the distribution of AL*Mexico

In several cases, the distribution of AL*Mexico, like that of AL*Naskapi, exhibits clear evidence of admixture between unrelated groups. For example, a single sample heterozygous for AL*Mexico drawn from an alleged fullblood southern Cheyenne Indian and the occurrence of AL*Mexico in the Apache and Navaho almost certainly represents admixture which, for whatever reason, was not acknowledged. AL*Mexico was relatively common in the Pima sample, as previously reported (e.g., Polesky et al., 1968; Johnston et al., 1969), but was absent in the Southern Uto-Aztecan group (Nahua) and in one (the Northern Paiute) of two groups of Northern Uto-Aztecan speakers. This is consistent with the marked genetic difference between Piman-speaking tribes and both northern and southern Uto-Aztecan tribes (Spuhler, 1979; Brown, 1988). A single individual from the Shoshone Snake tribe was heterozygous for AL*Mexico. Its presence in this Northern Uto-Aztecan tribe is consistent with an earlier report of its presence in one member of a Ute tribe (Johnston et al., 1969) and confirms the (rare) presence of AL*Mexico in the Northern branch of Uto-Aztecan. Since Proto-Northern Uto-Aztecan is about 3,000 years old and contains agriculture-related cognates shared with Southern Uto-Aztecan, both agriculture and the Uto-Aztecan language probably reached the area from Mesoamerica at about that time (Hill, 1999). While AL*Mexico appears to have been present in some, but not all, tribes of the Southwest U.S. for a very long time, its distribution and history within tribes speaking languages of the Shoshonean (Northern) branch (e.g., Ute, Paiute, Shoshone) of Uto-Aztecan, which appears to be much more limited, need to be better documented.

Three of the four tribes representing the Upland division of the Pai branch of the Yuman language group carried three or more samples heterozygous for AL*Mexico, and one sample heterozygous for AL*Mexico was found in Pai Pai, the other division of the Pai branch. This represents the first report of albumin phenotypes of Upland Yuman groups and of any Native Americans of Baja California, both of whom are less likely than Yumans of the upper Colorado River Valley that have been previously studied to have experienced very recent contact with Piman-speaking groups. Our discovery of nine Quechan sera, among the 143 screened, heterozygous for AL*Mexico is consistent with its reported presence in three other Yuman tribes of the River branch (Schell and Blumberg, 1988); two members of the Kiliwa tribe that were heterozygous for AL*Mexico establish the presence of the variant in a closely related tribe that some (e.g., Kendall, 1983) in fact have argued actually represents a branch of the Yuman language. While the variant was not found in either Baja tribe (Kumiai and Cucapa) representing another (the Delta) division of Yuman, previous reports of its presence in the Cocopa of Arizona indicate that AL*Mexico occurs in all three (or four) branches of Yuman and, therefore, probably predates the subdivision of that language

group, which occurred, at most, 1,000 years BP (Kaufman, 1988). AL*Mexico was found to be absent in the Cochimi, whose language and geographical proximity are closer than any other tribe (excepting Kiliwa) to the Yuman-speaking groups (Kendall, 1983), and in the Washo, whose language some linguists (e.g., Mixco, 1978) assign to the same branch of the Hokan language family as Yuman. The close relationship between the Cochimi, Kiliwa, and Yuman languages suggests that Yuman probably originated in Baja California and then diffused northward up the Colorado River to the Southwest U.S. no earlier than 1,000 years BP (Kaufman, 1988).

It is significant that the mtDNA haplogroup distributions of Uto-Aztecans of the American Southwest, while almost identical to that of Yumans as well as several other Southwest U.S. groups speaking mutually unrelated languages, are statistically significantly different from those of both the Nahua (a language of the Southern branch of the Uto-Aztecan language family) and Northern Paiute/Shoshone groups, members of the Northern branch of the Uto-Aztecan language family (see Table 2). Thus, when only Piman (i.e., Central Uto-Aztecan) sequences were compared with those of Yuman, the average number of paired differences between Uto-Aztecan and Yuman (see Table 2) declined from 7.14 (based on 80 paired comparisons) to 6.0 (based on 16 paired comparisons), lower than all but one of the 15 paired values in Table 2. The presence of AL*Mexico in the ancient and remote Yuman groups of Baja California that probably experienced minimal contact with most non-Yuman-speaking groups until the last millennium, the genetic similarity, but linguistic dissimilarity, of those groups to Pimans in the area (and the genetic dissimilarity of Pimans to Uto-Aztecans to both the North and South), and the lack of equilibrium between the albumin and mtDNA genotypes in Yumans, but not Pimans, suggest that the Pimans might have experienced relatively recent and intense admixture with Yuman-speaking peoples.

Archaeological and ethnographic evidence identifies the prehistoric precursors of the modern Pima/Papago and Yuman cultures as, respectively, the Hohokam culture of Southern Arizona/Mexican Sonora and the Hakatayan culture, centered in the Colorado River Valley (Willey, 1966). Some have argued that the Hohokam themselves were immigrants from Mexico (see Gumerman and Haury (1979) for a review of these arguments) and represented a "wave of advance" carried by population expansion associated with the emergence of agriculture (Renfrew, 1987; Bellwood, 1994, 1999). However, any unmodified version of this hypothesis is falsified by the general absence of haplogroup A, the most common haplogroup in Mesoamerica, in non-Athapaskan tribes of the American Southwest. Others have long argued that Hakatayan pottery is derivative of Hohokam (red-on-buff) pottery (Gladwin and Gladwin, 1930; Kroeber, 1939). This underlies the argument by Schroeder (1963) that Hohokam culture was simply a transformation of the indigenous Hakatayan culture stimulated by significant influences including maize cultivation, canal irrigation, platform mounds, ball courts, pottery human figurines, cotton cloth, human cremations, and copper bells from Central Mexico, beginning prior to 3,000 YBP and continuing through about 800 YBP. Proto-Yuman was probably spoken throughout this entire time period and began diversifying only after the demise of Hohokam culture during the last millennium.

Shaul and Hill (1998) used linguistic evidence to argue that the ancestors of both the Pimans and Yumans, and, much later, the Zuni as well, all of whom exhibit AL*Mexico, very high frequencies of mtDNA haplogroup B, and the near absence of mtDNA haplogroup A, participated in a common multiethnic, bilingual Hohokam culture. Hill (1999) argued that the above cultural influences that precipitated the development of Hohokam were brought to the American Southwest by Southern Uto-Aztecan emigrants from Mexico. The results of our study are consistent with this interpretation, suggesting that AL*Mexico originated in Mesoamerica, where it is found

among a variety of widely geographically dispersed tribes speaking unrelated languages, and then subsequently reached the American Southwest via the Tepiman corridor (Wilcox, 1986), i.e., the same route and migration by which maize agriculture (Haury, 1962; Matson, 1999), and probably also the Uto-Aztecan language (Romney, 1957; Fowler, 1983), reached the American Southwest. The language of economically superordinant immigrants has often been adopted, along with the culture and technology that accompany it, by economically subordinant hunter/gatherers (Bloomfield, 1935). While cultural influences clearly moved from Mesoamerica northward to the American Southwest, the near-absence of mtDNA haplogroup A (the most common haplogroup among Uto-Aztecan-Speakers in Mesoamerica), among non-Athapaskans in the American Southwest (Lorenz and Smith, 1996), precludes a significant flow of maternally inherited genes northward along the Tepiman corridor. Prehistoric studies of mtDNA extracted from Anasazi (Carlyle et al., 2000) and Freemont (Parr et al., 1996) skeletal material in the Southwest confirm the long-term persistence of a very low frequency of haplogroup A and high frequency of haplogroup B in that area, unlike Mesoamerica (Lorenz and Smith, 1997). However, the ubiquitous presence of haplogroup B and the general paucity of haplogroup A in the American Southwest and the much lower frequency of haplogroup B and high frequency of haplogroup A in Mesoamerica are compatible with either a northerly flow of predominantly male emigrants from Mexico along the Tepiman corridor or their subsequent retreat to Mesoamerica after the collapse of Hohokam culture about 600 years ago. If the former is true, the Y chromosome haplotypes should exhibit far greater similarities among the Northern, Central, and Southern Uto-Aztecan speakers than do the mtDNA haplotypes described here. If the latter is true, the prehistoric remnants of these Mexican emigrants with a high frequency of mtDNA haplogroup A (thus, clearly neither the Anasazi nor Freemont) should be demonstrable in other prehistoric skeletal populations from the area such as the Hohokam, whose dental morphology more closely resembles that of modern Mesoamericans than modern Southwesterners (Turner, 1993). In light of the evidence that Pimans, but not Yumans, adopted a language imported from Mesoamerica along with agriculture (Hill, 1999), the proposition that the nonagricultural tribal groups speaking Shoshonean languages are more closely related to some non-Uto-Aztecan-speaking tribes than to (Nahuatlan-speaking) Aztecans should also be carefully examined. It is possible that close study of the distribution of other rare mutations of New World origin, in light of what is known or hypothesized about historic movements of Native American groups, can enlighten our understanding of population prehistory. Of course, caution should always be exercised in interpreting distributions of single rare genes, especially when sample sizes are not large.

CONCLUSIONS

The distribution of AL*Naskapi encompasses groups speaking a number of languages not known to be related. Geographically, it is most widespread among Algonquian-speaking groups that share a common protolanguage spoken at least 4,000 years BP which is, therefore, a minimum date for the origin of AL*Naskapi. Since this predates the divergence of Athapaskans and marks the emigration of Algonquians from the Columbia Plateau, common ancestry between Algonquians and Athapaskans must explain the ubiquity of AL*Naskapi in both groups. This provides support for the hypothesis that a single migration provided the founder population for both groups. The marked differences in the incidence of AL*Mexico and mtDNA haplogroup distributions among the tribal groups speaking the three main branches of the Uto-Aztecan language family suggest that they are not closely genetically related. Genetic studies should be designed to test the hypothesis proposed here that predominantly male gene flow from Mesoamerica brought agriculture, Uto-Aztecan speech, and AL*Mexico to the American Southwest. The results of this study clearly caution against the equation of languages and demes.

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LITERATURE CITED

Allen L. 1931. Siouan and Iroquoian. Int J Am Ling 6:185–193.

Bellwood P. 1997. Prehistoric cultural explanations for widespread linguistic families. In: McConnell P, Evans N, editors. Archaeology and linguistics: Aboriginal Australia in global perspective. Melbourne: Oxford University Press. p 123–134.

Bellwood P. 1999. Austronesian prehistory and Uto-Aztecan prehistory: similar trajectories? University of Arizona Department of Anthropology Lecture series. January 27, Tucson, Arizona.

Bianchi NO, Bailliet G. 1997. Further comments on the characterization of founder Amerindian mitochondrial haplotypes. Am J Hum Genet 61:244–246.

Bloomfield L. 1935. Language. London: Allen and Unwin.

Brennan SO, Arai K, Madison J, Laurell C-B, Galliano M, Watkins S, Peach R, Myles T, George P, Putnam FW. 1990. Hypermutability of CpG dinucleotides in the propeptide encoding sequence of the human albumin gene. Proc Natl Acad Sci USA 87:3909–3913.

Brown KS, Johnson RS. 1970. Population studies on southwestern Indian tribes. III. Serum protein variations of Zuni and Papago Indians. Hum Hered 20: 281–286.

Brown KS, Alana BL, Dahlberg AA, Strandkov HH. 1958. The distribution of blood group alleles among Indians of Southwest North America. Am J Hum Genet 10:175–195.

Brown MD, Hosseini SH, Torroni A, Bandelt H-J, Allen JC, Schurr TG, Scozzari R, Cruciani F, Wallace DC. 1998. mtDNA haplogroup X: an ancient link between Europe/Western Asia and North America? Am J Hum Genet 63:1852–1861.

Brugge DM. 1983. Navaho. In: Ortiz A, editor. Handbook of North American Indians, Southwest, volume 10. Washington, DC: Smithsonian Institution.

Campbell L. 1997. American Indian languages: the historical linguistics of Native America. New York: Oxford University Press.

Campbell L, Mithun M. 1979. Introduction: North American Indian historical linguistics in current perspective. In: Campbell L, Mithun M, editors. The languages of Native America: a historical and comparative assessment. Austin: University of Texas Press. p 3–69.

Carlyle SW, Parr PL, Hayes MG, O'Rourke D. 2000. The context of maternal lineages in the greater Southwest. Am J Phys Anthropol (in press).

Cavalli-Sforza LL, Piazza A, Menozzi P, Mountain J. 1988. Reconstruction of human evolution: bringing together genetic, archaeological and linguistic data. Proc Natl Acad Sci USA 85:6002–6006.

Chafe WL. 1973. Siouan, Iroquoian and Caddoan. Curr Trends Ling 10:1164–1209.

Cleve H, Kirk RL, Parker WC, Bearn AG, Schacht LE, Kleinman H, Horsfail WR. 1963. Two genetic variants of the group-specific component of human serum: Gc Chippewa and Gc Aborigine. Am J Hum Genet 15: 368–379.

Comas D, Calafell F, Mateu E, Perez-Lezaun A, Bertranpetit A. 1996. Geographic variation in human mitochondrial DNA control region sequence: the population history of Turkey and its relationship to the European populations. Mol Biol Evol 13:1067–1077.

Davis I. 1989. A new look at Aztec-Tanoan. In: Key MR, Hoenigswald HM, editors. General and Amerindian ethnolinguistics: in remembrance of Stanley Newman. New York: Mouton de Gruyter. p 365–380.

Denny JP. 1991. The Algonquian migration from Plateau to Midwest: linguistics and archaeology. In: Cowan W, editor. Papers of the 22nd Algonquian Conference. Ottawa: Carleton University.

Drucker P. 1995. Cultures of the North Pacific Coast. San Francisco: Chandler.

Fowler CS. 1983. Some lexical clues to Uto-Aztecan prehistory. Int J Am Ling 49:224–257.

Franklin SG, Wolf SI, Ozdemir Y, Yuregir GT, Isbin T, Blumberg BS. 1980. Albumin Naskapi variant in North American Indians and Eti Turks. Proc Natl Acad Sci USA 77:5480–5482.

Gladwin W, Gladwin HS. 1930. Some Southwestern pottery types, series I. Gila Pueblo Medallion Papers, no. 8, Globe, Arizona.

Goddard I. 1994. The west-to-east cline in Algonkian dialectology. In: Cowan W, editor. Papers of the 25th Algonquian Conference. Carleton, Canada: Carleton University Press. p 187–211.

Goddard I. 1996. The classification of the Native Languages of North America. In: Goddard I, editor. Handbook of North American Indians, Volume 17. Languages. Washington, DC: Smithsonian Institution. p 75–90.

Greenberg JH. 1987. Language in the Americas. Stanford: Stanford University Press.

Gumerman GJ, Haury EW. 1979. Prehistory: Hohokam. In: Ortiz A, editor. Handbook of North American Indians, volume 9. Southwest. Washington, DC: Smithsonian Institution. p 75–90.

Haury E. 1962. The Greater American Southwest. In: Braidwood RJ, Willey GR, editors. Courses toward urban life: some archaeological considerations of cultural alternates. New York: Viking Fund Publications in Anthropology. p 10–131.

Hill JH. 1999. Why is Uto-Aztecan so big? University of California at Davis Anthropology Colloquium Series, May 24, Davis, California.

Holbrook IB, Leaver AG. 1976. A procedure to increase the sensitivity of staining by Coomassie brilliant blue G250-perchloric acid solution. Anal Biochem 75:634–636.

Huss KF, Putnam W, Takahashi N, Takahashi Y, Weaver FA, Peters T. 1988. Albumin Coopersform: a serum albumin variant with the same (323 Lys → Asn) mutation found in albumins in Italy and New Zealand. Clin Chem 34:183–187.

Johnston FE, Blumberg BS, Agarwal SS, Melartin L, Burch TA. 1969. Alloalbuminemia in southwestern U.S. Indians: polymorphism of albumin Naskapi and Albumin Mexico. Hum Biol 41:263–270.

Karafet TM, Zegura SL, Posukh O, Osipova L, Begen A, Long J, Goldman D, Klitz W, Harihara S, Knijff P, Wiebe V, Griffiths RC, Templeton AR, Hammer MF. 1999. Ancestral Asian source(s) of New World Y-chromosome founder haplotypes. Am J Hum Genet 64:817–831.

Kaufman T. 1988. A research program for reconstructing Proto-Hokan: first groupings. Unpublished manuscript, University of Pittsburgh.

Kaur H, Franklin SG, Shrivastava PK, Blumberg BS. 1982. Alloalbuminemia in North India. Am J Hum Genet 34:972–979.

Kendall MB. 1983. Yuman languages. In: Ortiz A, editor. Handbook of North American Indians, volume 10. Southwest. Washington, DC: Smithsonian Institution. p 4–24.
Kinkade MD. 1990. History of research in linguistics. In: Shuttles W, editor. Handbook of North American Indians, volume 7. Northwest Coast. Washington, DC: Smithsonian Institution. p 98–106.
Krauss ME. 1973. Na-Dene. Curr Trends Ling 10:950–953.
Kroeber AL. 1939. Culture and natural areas of native North America. University of California publications in American archaeology and ethnology, volume 38. Berkeley: University of California.
Leer J. 1990. Tlingit: a portmanteau language family? In: Baldi P, editor. Linguistic change and reconstruction methodology. Berlin: Mouton de Gruyter.
Lisker R, Cobo L, Mora G. 1971. Distribution of albumin variants in Indians and non-Indians of Mexico. Am J Phys Anthropol 35:119–124.
Lorenz J, Smith DG. 1994. Distribution of the 9-bp mitochondrial DNA region V deletion among North American Indians. Hum Biol 66:777–788.
Lorenz J, Smith DG. 1996. mtDNA variation among Native Americans: geographic and ethnic distribution of the four founding mtDNA haplogroups. Am J Phys Anthropol 101:307–323.
Lorenz J, Smith DG. 1997. Distribution of sequence variation in the mtDNA control region of Native North Americans. Hum Biol 69:749–776.
Matson RG. 1999. The spread of maize to the Colorado Plateau. Archaeol Southwest 13:10–11.
Melartin L, Blumberg BS. 1966. Albumin Naskapi: a new variant of serum albumin. Science 153:1664–1666.
Melartin L, Blumberg BS, Lisker R. 1967. Albumin Mexico, a new variant of serum albumin. Nature 215: 1288–1289.
Merriwether DA, Rothammer F, Ferrell RE. 1995. Distribution of the four founding lineage haplotypes in Native Americans suggests a single wave of migration for the New World. Am J Phys Anthropol 98:411–430.
Miller WR. 1984. The classification of the Uto-Aztecan languages based on lexical evidence. Int J Am Ling 50:1–24.
Mixco MJ. 1978. Cochimi and Proto-Yuman: lexical and syntactic evidence for a new language family in Lower California. Anthropological papers no. 101. Salt Lake City: University of Utah.
Nei M, Tajimo F, Tateno Y. 1983. Accuracy of estimated phylogenetic trees from molecular data. II. Gene frequency data. J Mol Evol 19:153–170.
Nichols J. 1992. Linguistic diversity in space and time. Chicago: University of Chicago Press.
Nichols J. 1998. The first four discoveries of America: linguistic evidence. Paper presented at the annual meeting, American Association for the Advancement of Science, February.
O'Rourke DH, Mobarry A, Suarez BK. 1992. Patterns of genetic variation in Native America. Hum Biol 64: 417–434.
Parr RL, Carlyle SW, O'Rourke DH. 1996. Ancient DNA analysis of Freemont Amerindians of the Great Salt Lake wetlands. Am J Phys Anthropol 99:507–518.
Polesky HF, Rokala DA, Burch TA. 1968. Serum albumin polymorphism in Indians of Southwestern United States. Nature 220:175–176.
Rankin RL. 1993. On Siouan chronology. Paper presented at the Annual Meeting of the American Anthropological Association, Washington, DC.
Renfrew C. 1987. Archaeology and language: the puzzle of Indo-European origins. London: Jonathan Cape. 346 p.
Romney AK. 1957. The genetic model and Uto-Aztecan time perspective. Davidson J Anthropol 3:35–41.
Sapir E. 1929. Central and North American languages. In: Encyclopaedia Britannica, volume 5, 14th ed. London and New York: Encyclopaedia Britannica Co. p 138–141.
Schell LM, Blumberg BS. 1988. Alloalbuminemia and the migrations of native Americans. Yrbk Phys Anthropol 31:1–13.
Schell LM, Agarwall SS, Blumberg BS, Levy H, Bennett PH, Laughlin WS, Martin JP. 1978. Distribution of albumin variants Naskapi and Mexico among Aleuts, Frobisher Bay Eskimos, and Micmac, Naskapi, Mohawk, Omaha, and Apache Indians. Am J Phys Anthropol 49:111–117.
Schroeder AH. 1963. Hakataya, Patayan and Hohokam. Regional research abstract, no. 308. Santa Fe: National Park Service.
Shaul DL, Hill JH. 1998. Tepimans, Yumans and other Hohokams. Am Antiq 63:375–396.
Siebert FT Jr. 1967. The original home of the proto-Algonquian people. Anthropological series 78. Natl Mus Can Bull 214:13–47.
Siegel S, Castellan NJ Jr. 1988. Nonparametric statistics for the behavioral sciences. New York: McGraw-Hill, Inc.
Smith DG. 1980. Paternity exclusion in six captive groups of rhesus monkeys (*Macaca mulatta*). Am J Phys Anthropol 53:243–249.
Smith DG, Malhi RS, Eshleman J, Lorenz JG, Kaestle FA. 1999. Distribution of mtDNA haplogroup X among Native North Americans. Am J Phys Anthropol 110:271–284.
Spuhler JN. 1979. Genetic distance, trees, and maps of North American Indians. In: Laughlin WS, Harper AB, editors. The first Americans: origins, affinities and adaptations. New York: Gustav Fischer. p 135–183.
Stone AC, Stoneking M. 1998. mtDNA analysis of prehistoric Oneota population: Implications for the peopling of the New World. Am J Hum Genet 62:1153–1170.
Suarez BK, Crouse JD, O'Rourke DH. 1985. Genetic variation in North American Amerindian populations: the geography of gene frequencies. Am J Phys Anthropol 67:217–232.
Swadesh M. 1953a. Mosan I: a problem of remote common origin. Int J Am Ling 19:26–44.
Swadesh M. 1953b. Mosan II: comparative vocabulary. Int J Am Ling 19:223–236.
Swadesh M. 1971. The origin and diversification of language. Chicago: Aldine-Atherton.
Szathmary EJ. 1993. Genetics of aboriginal North Americans. Evol Anthropol 1:202–220.
Szathmary EJE, Auger F. 1983. Biological distances and genetic relationships within Algonkians. In: Steegmann AJ Jr, editor. Boreal forest adaptations. New York: Plenum Press. p 289–315.
Takahashi N, Takahashi Y, Blumberg BS, Putnam FW. 1987. Amino acid substitutions in genetic variants of human serum albumin and in sequences inferred from molecular cloning. Proc Natl Acad Sci USA 84: 4413–4417.
Torroni A, Schurr TG, Yang CC, Szathmary EJE, Williams RC, Schanfield MS, Troup GA, Knowler WC, Lawrence DN, Weiss KM, Wallace DC. 1992. Native American mitochondrial DNA analysis indicates that the Amerind and the Nadene populations were

founded by two independent migrations. Genetics 130:153–162.
Turner CG II. 1993. Southwest Indian teeth. Natl Geogr Res Explor 9:32–53.
Whorf BL, Trager GL. 1937. The relationship of Uto-Aztecan and Tanoan. Am Anthropol 39:609–624.
Wilcox DR. 1986. The Tepiman connection: a model of Mesoamerican-Southwestern interaction. In: Mathien FJ, McGuine RH, editors. Ripples in the Chichimec sea: new considerations of Southwestern-Mesoamerican interactions. Carbondale: Southern Illinois University Press. p 135–153.
Willey GR. 1966. An introduction to American archaeology. I. North and Middle America. Englewood Cliffs, NJ: Prentice-Hall.
Wormington HM. 1970. Prehistoric Indians of the Southwest. Denver: Denver Museum of Natural History.